GAMETOPHYTIC DEVELOPMENT OF BLISTER RUSTS[1]

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(WITH FOUR FIGURES)

Since the discovery of the pycnial stages for the stem forms of blister rusts on pines, several interesting points have arisen with respect to their alternation with the aecial stage. The pycnial stage of rusts on Angiosperms usually precedes the appearance of the subsequent stage (aecia, primary uredinia, or telia) by a few days to several weeks. The interval of time in completing the gametophytic development in the case of the stem rusts on pines is materially different.

Weir and Hubert (9) have added much to our knowledge regarding the appearance of pycnia of several blister rusts. Pycnia of *Cronartium cerebrum* on *Pinus Banksiana* were collected as early as May 12, 1916. Four of the galls developed aecia within 4 or 5 mm. from the pycnial exudations on the same galls, but not from identical pycnial areas. The pycniospores of *C. Comptoniae* developed similarly to those of *C. Comandrae* in respect to their appearance on previously unruptured tissue. They secured exudation of pycniospores by laboratory forcing methods from specimens collected on May 12, 1916, at Cass Lake, Minnesota. They report as follows:

> In *Cronartium coleosporoides* the pycniospores are produced on old galls previously ruptured, as well as on unruptured infected tissues . . . . In a period from April 4 to 15, 1916, abundant pycnial exudations containing pycniospores were obtained from galls of *C. coleosporoides* . . . . The pycniospores of *C. Comandrae* apparently develop but once on the same tissue preceding the appearance of the aeciospores. The production of aecia kills the infected tissues which are included in the aecial ruptures. The tissues bordering this area are invaded by the mycelium of the fungus, produce swellings, and give rise to pycniospores, either in early spring or in late summer and fall, whenever sufficient time has elapsed from the last production of aecia. In the cases recorded the pycniospores appeared in the same season following the production of aecia, with only five months intervening, but not from the identical area from which the pycnia were produced.

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BOYCE (2) first observed the pycnia of *Peridermium pyriforme* on *Pinus ponderosa* near Castella, Shasta County, California, July 21, 1916. He states that "the pines are probably infected in the summer or fall of one season, pycnia do not appear until the summer of the next season at the earliest, while mature aecia are produced in the late spring or early summer of the third season."

HEDGCOCK, BETHEL, and HUNT (6) state that the pycnia of *Peridermium pyriforme* are borne on areas of the bark of pines contiguous to the aecia and preceding them by one year. They are produced in the portions most recently invaded, commonly on the trunks and limbs. In both *P. pyriforme* and *P. filamentosum* the pycnia most frequently appear at a date later in the season than the aecia.

HEDGCOCK and LONG (7), from field observations during a period of four years, find that in the swellings of *Peridermium cerebrum* or *Pinus virginiana* the pycnia precede the aecia one year, instead of preceding them during the same spring. In other words, the pycnia and aecia occur during alternate years, and two years is the time required for a life cycle of all forms of spores of the rusts.

DODGE and ADAMS (5) studied material of *P. cerebrum* on *Pinus rigida* and *P. virginiana*, and our observations indicate that there is an alternation of aecia and pycnia.

> We have not seen in any instance spermatial hyphae developing in the tissue overlying that in which the aecidia are being formed. Cross-sections of the Virginia material developing both spermatial and aecidial fructifications on the same gall show that there is no sharp line of demarcation between the two. In one burl there was a space of only 700 μ separating them.

SHIRAI (8) has shown by culture experiments the connection of *Peridermium giganteum* and *Cronartium quercuum*, which has been considered the same as the form of *P. cerebrum* in North America. In an illustration he shows the extended pycnial layer in the tissue overlying the aecia, and states:

> The spermagonia of this fungus are formed in the month of January in the intercellular spaces between the corky bark and the cortical parenchyma. . . . . In consequence of the formation of the spermagonia and the subsequent cracking of the corky bark, the pressure of the latter on the inner bark greatly lessens, and thus secures the formation of the aecidial layers in the deeper tissues.

I have examined specimens of *Peridermium Strobi* collected May 5 and 21, 1917, in New Hampshire by Dr. L. O. OVERHOLTS. The specimens were in sporulating condition. In every instance the mature pycnial layer was found intact in the tissue overlying the aecia. COLLEY also states that "the pycnia of *Cronartium ribicola* precede the aecia by at least one growing season on any given area of infection, and succeeding generations of pycnia and aecia follow a more or less definite schedule." In this case the perennial infection is not restricted, as found with some other stem rusts. It is a typical progressive infection. The development of pycnia and aecia of the leaf rusts of conifers apparently is correlated with the time of infection. In the case of *Peridermium acicolum* mature spermagonia have been found as early as March 1, and the aecial primordia developing May 25, 1917, only an interval of about three months intervening between the appearance of pycnia and aecia. The infection of the needles occurs the preceding fall. Mature aecia of *Peridermium Peckii* were collected May 20, 1917, at Pine Grove Mills, Center County, Pennsylvania. The pycnia precede the aecia by two to three weeks, according to field observations. The same condition occurs in *Coeoma Abietis-canadensis*, which is found on the cones and new terminal growth of *Tsuga canadensis*. The infection with these two species occurs the same spring. These observations indicate that with respect to the seasonal interval there are at least three methods in the sequence of pycnia and aecia (or the completion of the gametophytic development on any given infected area).

1. The first method is the alternation of pycnia and aecia in *Peridermium cerebrum*, as reported by HEDGCOCK and LONG (7), and DODGE and ADAMS (5). The evidence supports the contention that it takes two years to complete the gametophytic period of development on any given infected area. The pycnia appear in spring and are sloughed off about the middle or end of the same growing season. The following spring the aecia are developed. It is not until the third season that the pycnia again are developed. This condition may occur on the same gall, in which case apparently one part is an older infection. It is usually found that such areas represent different stages of maturity, and are differentiated by furrows.

Whether the form of *Peridermium cerebrum* is the same as *P. giganteum* remains to be established. SHIRAI describes as well as illustrates the pycnia in the tissue overlying the aecia, which would not agree with our observations on the American form. It is possible that environmental conditions may be concerned in this instance.

2. The second method is that in which maturity of the pycnia precedes the aecia in adjacent as well as the overlying tissue within a period of about six months. The full cycle of development of pycnia and aecia on the coniferous host in the same area is completed within a period of twelve months. In contrast with the first method the pycnia and aecia are sloughed off at the same time. The writer (1) has shown that the pycnia occur in the tissue overlying the aecia in *Peridermium Comptoniae* and *P. pyriforme*. Being sloughed off at the same time indicates there is no alternation as found with *P. cerebrum*. It was not known when the pycnia developed, since the exudation of pycniospores was never observed in the field when this material was collected. The presence of the pycnial layer, however, could be recognized by carefully removing the bark. At this time the pycnia appeared as an extensive olive green layer, irregular in outline, and mature. On October 17, 1919, in the vicinity of State College several infections of *Peridermium Comptoniae* on *Pinus virginiana* were observed with exudations of pycniospores. Their appearance was similar to the description given by WEIR and HUBERT. On removing the bark the pycnial layer was lemon yellow in color. Cross-sections showed the usual extensive crustlike layer of the pycnia. There were extensive pycnial primordia which indicate the immature development of the pycnial layer. From these observations and others it would appear that *P. Comptoniae*, *P. pyriforme*, *P. coleosporoides*, and *P. Strobi* represent a group of species in which the pycnia and aecia complete their period of development within twelve months. No doubt certain environments or other conditions may alternate the period of time the pycnia may appear in one season, but it seems probable that this sequence is more or less regular after the first period of development has been completed. The completion of the initial gametophytic period of development

appears to be variable. CLINTON (3, 4) has shown, by infection of white pines with telia of *Cronartium ribicola,* that the pycnia may appear with the initial infection after a period of six months, one year, two years, and sometimes three years.

3. The third method is found with the leaf rusts of conifers when the period of development is completed within one growing season. This is similar to the period of pycnial and aecial development of Angiosperms. I have found mature pycnia of *Peridermium acicolum* March 1, 1917, at Pine Grove Mills, Center County, Pennsylvania, while mature aecia were collected May 25, 1917. In the case of *P. Peckii* the pycnia were observed to precede the aecia by only two or three weeks; this difference may be correlated with the time of infection. With *P. acicolum* infection occurs in the fall; while with *P. Peckii* infection occurs after the new growth is developed in the spring.

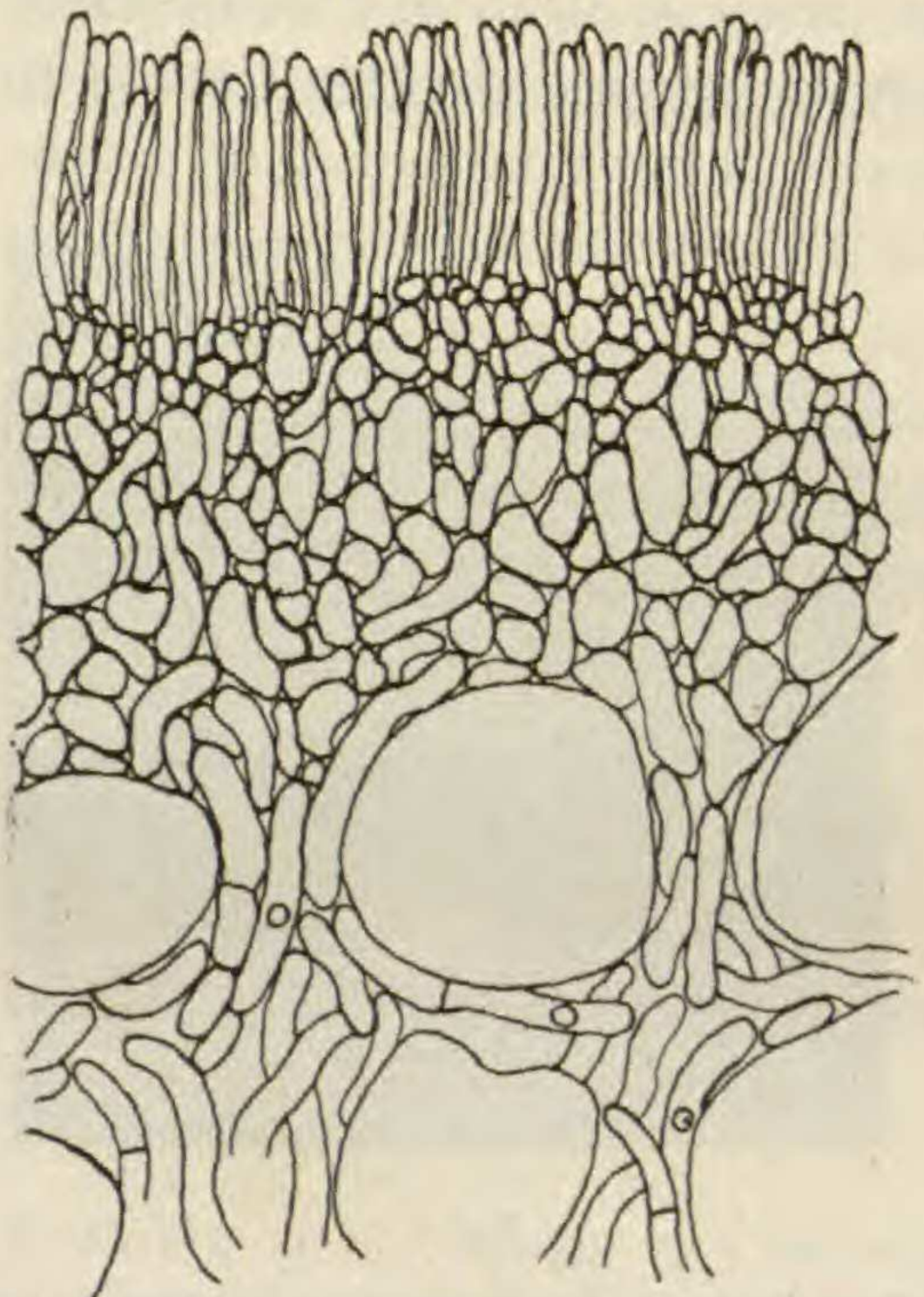

FIG. 1

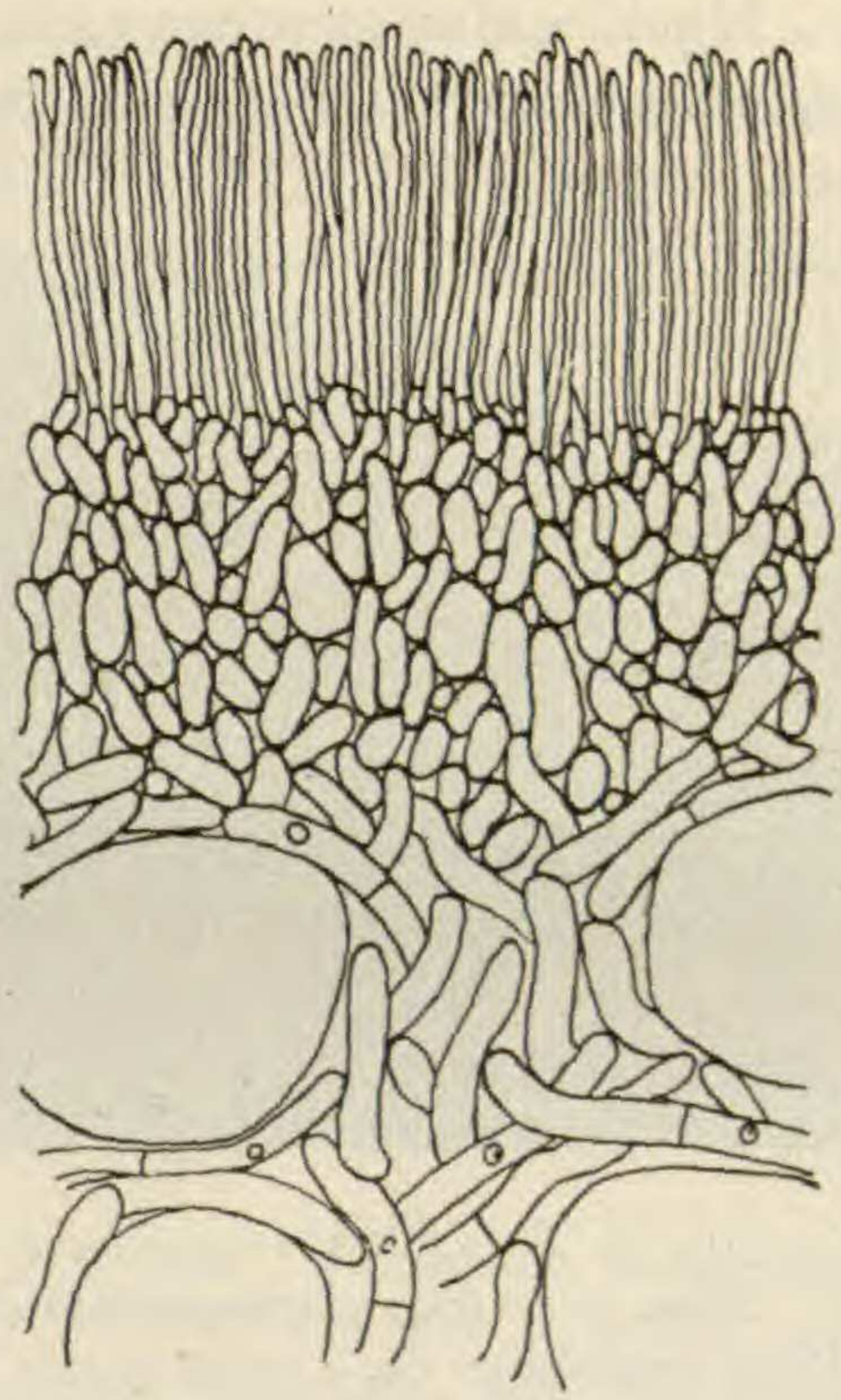

FIG. 2

FIGS. 1, 2.—Fig. 1, cross-section of pycnial layer of *Peridermium Comptoniae* on *Pinus virginiana;* fig. 2, cross-section of pycnial layer of *Peridermium cerebrum* on *Pinus rigida;* drawn with camera lucida at same magnification.

The first method is in striking contrast with the usual pycnial and aecial relation of rusts on the Angiosperms; the second method appears to be intermediate; while the third method apparently is the one most prevalent with all species of rust. Perennial infection on the Angiosperms is found to complete the gametophytic development in one season, regardless of being heteroecious or autoecious.

Much confusion arises as to the determination of *Peridermium cerebrum* and *P. Comptoniae* on certain species of pines, owing to

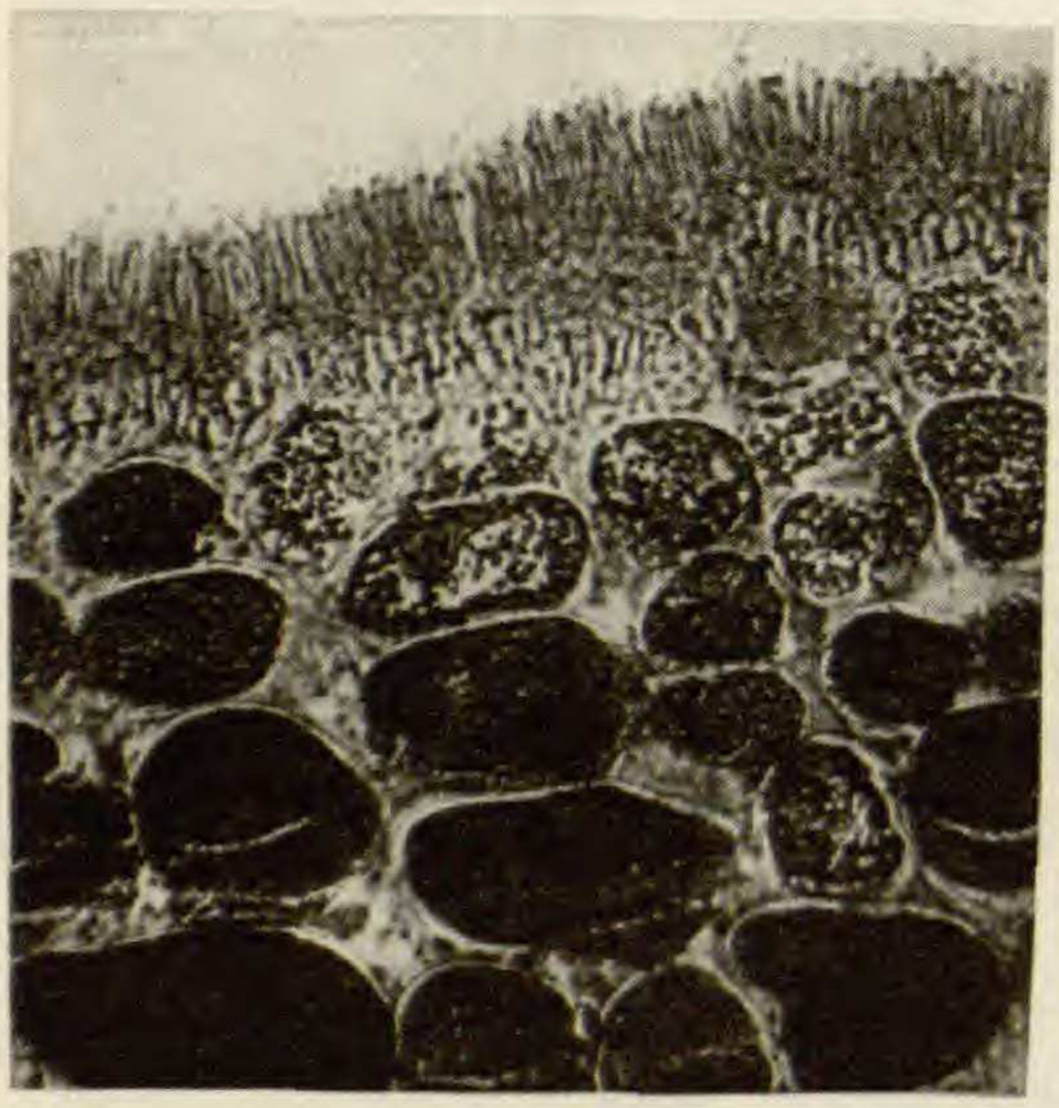

FIG. 3

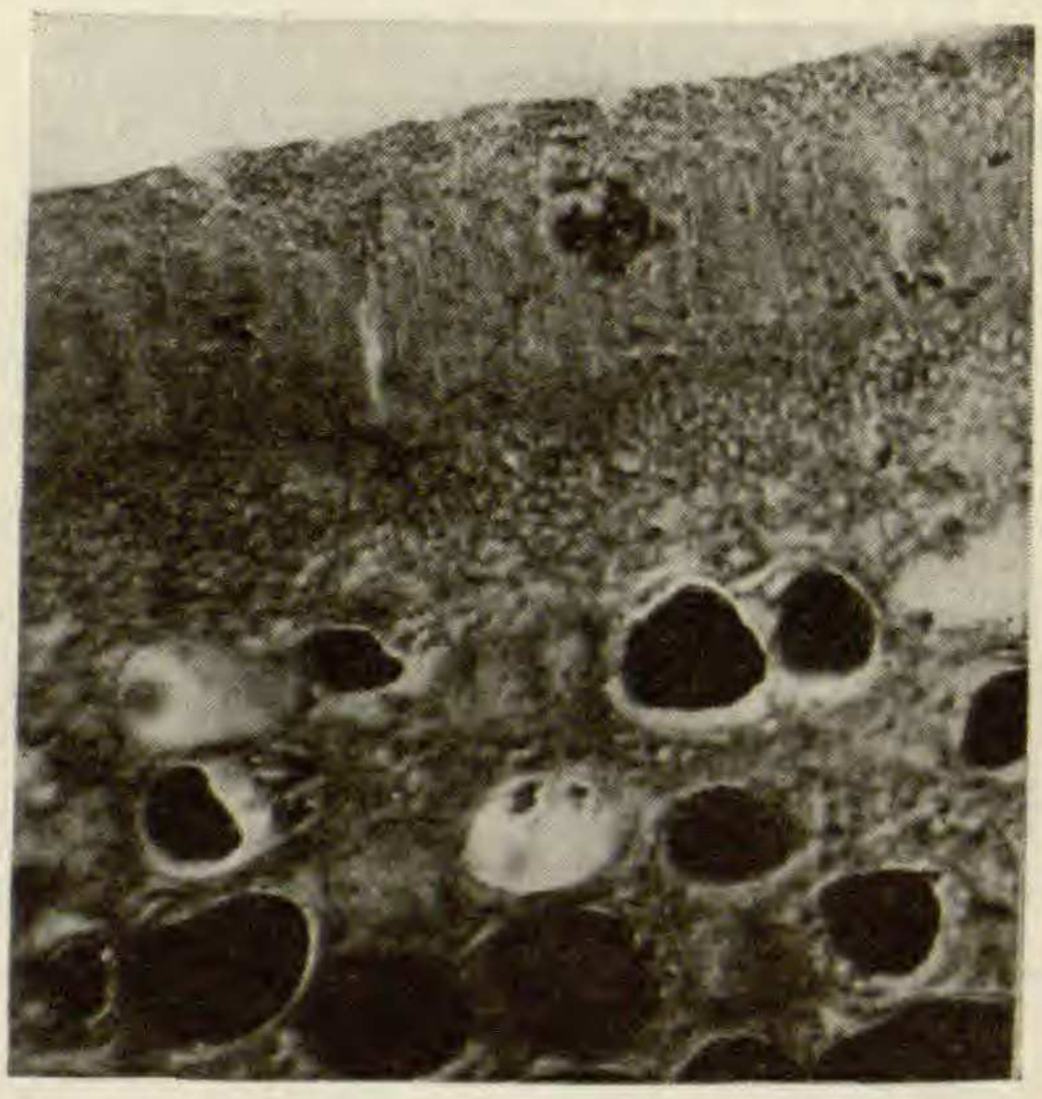

FIG. 4

FIGS. 3, 4.—Fig. 3, cross-section of pycnial layer of *Peridermium Comptoniae* on *Pinus virginiana;* fig. 4, cross-section of pycnial layer of *Peridermium cerebrum* on *Pinus rigida;* photomicrographs taken at same magnifications.

the similarity of infection upon the host. The types of infection are represented by fusiform, globoid, and semigloboid swellings. While the peridium and dehiscence of the aecia are good characters for differentiating these two species, it often occurs that specimens are immature or past their maturity for these characters to be depended upon. Under such conditions material collected in the spring or late summer may be differentiated by the pycnial characters. If the aecia are mature one can examine for the presence of pycnia in the overlying tissue. Providing pycnia are found, the form would agree with *P. Comptoniae;* if pycnia were absent, the form would agree with *P. cerebrum.* Exudation of pycniospores

does not have to be depended upon. The presence of pycnia is best determined by carefully removing the overlying bark from the cortex. The pycnia develop in the subcorticular tissue. Free-hand sections can easily be cut and mounted with a little dilute alcoholic eosin which provides a satisfactory means for examination. The pycniophores of *P. Comptoniae* are shorter and more uniform in diameter throughout their length than those of *P. cerebrum* (figs. 1–4). It is found that the pycniophores are longer and more tapering with *P. cerebrum.* No conspicuous difference in size could be found between the pycniospores of the two species. The following measurements for comparison are taken from killed material and stained with Fleming's Triple. The length of the pycniophores was taken from the sub-basal cell to the tip, and for *Peridermium Comptoniae* was 15–27 μ; while for *Peridermium cerebrum* it was 30–36 μ. A comparison of the pycniophores in these two species is shown in figs. 1 and 3, drawn at the same magnification.

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